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published in
Biological Cybernetics
2003

DOI (link to publisher)
10.1007/s00422-002-0379-1

document version
Publisher's PDF, also known as Version of record

Biol. Cybern. 88, 302–318 (2003)
DOI 10.1007/s00422-002-0379-1

Biological Cybernetics

Learning to juggle: on the assembly of functional subsystems into a task-specific dynamical organization

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Received: 11 February 2002 / Accepted: 12 November 2002 / Published Online: 7 April 2003

Abstract. We examined the development of task-specific couplings among functional subsystems (i.e., ball circulation, respiration, and body sway) when learning to juggle a three-ball cascade, with a focus on learning-induced changes in the coupling between ball movements and respiration and the coupling between ball movements and body sway. Six novices practiced to juggle three balls in cascade fashion for one hour per day for twenty days. On specific days (7 in total), ball movements, center-of-pressure (CoP) trajectories and respiration traces were measured simultaneously. Discrete, time-continuous and spectral analyses revealed that the spatio-temporal variability of the juggling patterns decreased with practice and that the degree to which the task constraints were satisfied increased gradually. No conclusive evidence was found for ball movement-respiration coupling. In contrast, clear-cut evidence was found for the presence of 1:3 and 2:3 frequency locking between the vertical component of the ball trajectories and both the anterior-posterior and the medio-lateral components of the CoP. Incidence and expression of these mode locks varied across individuals and altered in the course of learning. Gradual changes in locking strength, appearances and disappearances of mode locks, as well as abrupt transitions between coupled states were observed. These results indicate that dissimilar learning dynamics may arise in the functional embedding of subsystems into a task-specific organization and that motor equivalence is an inherent property of such emerging task-specific organizations.

1 Introduction

Skilled performance manifests itself in highly coherent yet flexible goal-directed behavior. It requires, among other things, that various subsystems are assembled in a task-specific manner. Identification of the principles governing such assembly processes poses a major challenge to human movement scientists. In addressing this problem, researchers have focused predominantly on the formation of task-specific synergies among body segments, joint angles and end-effectors (e.g., Arutyunyan et al. 1968, 1969; Newell and Van Emmerik 1989; Temprado et al. 1997; Zanone and Kelso 1992). Although coordination among effector components is a necessary requirement for achieving a certain task goal, it is usually not a sufficient one. Surely, when performing for instance a volleyball smash the ball needs to be hit at an appropriate time and place, implying a proper coordination among shoulder, elbow and wrist joints in the course of the action. Before being able to smash the ball, however, the player must perform a vertical jump, which requires the coordination of leg and hip joints as well as appropriate postural control during the various phases of the jump. In addition, visual information about the ball in flight and the evolving game situation, as well as proprioceptive information about the orientation of the body in space, have to be registered on-line. Thus, in general, the performance of complex perceptual-motor actions requires that multiple subsystems be organized in a task-specific and coherent manner. Presumably, the performance level of actors critically depends on such task-specific coordination among subsystems.

In view of such considerations, several authors have recognized that a comprehensive theory about the acquisition of perceptual-motor skills should include an account as to how the subsystems of the human action system become integrated into effective task-specific organizations. For instance, in a book that appeared only recently in English, Bernstein (1996) argued that the human body consists of a variety of functionally defined subsystems or 'levels in the construction of movement'. These are more or less specialized in performing certain subtasks. In order to become proficient (or 'dexterous') they have to be assembled in a task-specific and efficient manner, that is, in to functionally effective and resilient 'global organizations'. In a similar spirit, Bingham (1988) argued that the assembly of

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'task-specific devices' is 'shaped' by both the 'inherent' (i.e., permanent) dynamical properties of the subsystems and the 'incidental' dynamics introduced by the task. Although these are appealing and important theoretical notions, it is fair to say that, to date, the assembly of functional subsystems into effective task-specific organizations has hardly been investigated empirically, certainly not in the context of long-term learning processes involving the parallel integration of multiple subsystems. This is unfortunate as it may be expected that in-depth studies of the development of task-specific couplings among functional subsystems during the acquisition of perceptual-motor skills will be illuminating with regard to both the organization of specific task spaces and the dynamical features of processes of motor learning.

To begin filling this lacuna in the literature, we conducted an experiment aimed at examining the relations between ball movements and respiration and between ball movements and postural sway as novices practiced a standard 3-ball cascade pattern. In order to motivate this selection of subsystems and to formulate our expectations in this regard, we briefly discuss the theoretical perspective from which we set out to study this instance of perceptual-motor learning, followed by a summary of previously obtained insights into the learning of juggling, locomotion-respiration coupling and the effects of supra-postural task performance on body sway.

1.1 A dynamical systems perspective on the development of task-specific devices

We view the development of task-specific devices from the perspective of dynamical systems theory. Within this approach, two directions of theorizing about skill acquisition may be distinguished. In one, learning is understood as the evolution of a potential landscape describing the formation and annihilation of stable solutions of an already established collective variable for the to-be-learned coordination pattern (Schöner and Kelso 1988; Schöner et al. 1992; Zanone and Kelso 1992). For instance, in the paradigmatic experiment of Zanone and Kelso (1992), the subjects learned to oscillate their index fingers at a phase relation of $\pi/2$, a pattern that is typically unstable if unpracticed. Practice resulted in a gradual and lasting change of the stability properties of the so-called order parameter relative phase, not only of the acquired phase relation but of all possible phase relations.

The second line of inquiry focuses on changes in system dimensionality due to learning, that is, without assuming a priori the existence of a small number of order parameters. For instance, Haas (1995, see also Haken 1996), using principal component analysis, examined the changes in the number of variables that are minimally required for reconstructing the whole-body movement of novices learning to ride the pedalo. Initially, the 22D whole body movement vector could be effectively represented as a 5D system. As learning progressed, this number gradually decreased to 2. Similarly, using state-space reconstruction techniques, Mitra et al. (1998) reported a reduction in the dimensionality of the evolving dynamics as a function of practice in learning a bimanual coordination task. On the basis of these two studies, it appears that initial and intermediate levels of learning involve a reduction of the dimensionality of the underlying control structure.

Recently, (Scholz and Schöner 1999; Scholz et al. 2000) introduced a similar but arguably more probing approach, explicitly aimed at identifying the control structure for the task of interest. Revisiting the pistol-shooting task, they analyzed the variability in a high-dimensional joint configuration space in both successful and unsuccessful trials. Specifically, they showed that the low-dimensional configuration subspace, which left the task variable unaltered and was therefore called 'non-essential', was significantly more variable than the 'essential' subspace affecting the task variable. Apparently, the 'non-essential' variables can be released from control without deteriorating performance. The theoretical significance of this approach to skill acquisition as compared to its precursors is that it focuses on changes in the functional role of the variables of interest rather than merely on their number. Acquiring a complex perceptual-motor skill may now be viewed as a process of 'appreciating' or 'discovering' the 'essential' variables in a to-be-learned task.

The present study builds on this latter line of work in that it attempts to capitalize on the evolution of patterns of correlation in multivariate data-sets with the explicit goal of identifying the essential variables or components in the given, to-be-learned task. However, it follows from our research interest (see above), that in doing so, we cannot confine ourselves to the patterns of correlation as defined solely by the state variables of the end-effectors, but have to include measurements obtained from other, more remote, functional subsystems as well.

1.2 Juggling and its acquisition

Juggling is a complex perceptual-motor activity which is supported by various subsystems, such as visual, proprioceptive, and haptic systems, the manual control system for handling the balls, the postural control system for keeping the center-of-pressure (CoP) above the base of support and the respiratory system for supporting aerobic metabolic processes. Initial studies of the manual control system in juggling focused on the temporal variables over which Shannon (see Horgan 1990) defined his juggling theorem (see also Beek and Lewbel 1995), namely the dwell time of the balls in the hands the empty time of the hands and the flight time of the balls in the air (Beek 1989; Beek and Turvey 1992; Van Santvoord 1995). These studies have been instrumental in identifying possible principles governing the timing of 'key' events (i.e., throwing and catching) and in documenting changes in the temporal variability of juggling as a function of learning and expertise (e.g., Beek and Van Santvoord 1992; Van Santvoord and Beek 1996).

Recently, Post et al. (2000) focused on the variability of the juggling pattern using time-continuous correlation techniques that are well suited to study the degree of interaction between time-continuous processes and thus avoiding a priori assumptions regarding the relevance of certain time-discrete events. Post et al. showed analytically that, due to the symmetries involved in the originally 6D juggling pattern (three $2\pi/3$ rad phase lagged ball evolutions $\times$ two dimensions, horizontal and vertical, which are 1:2 frequency locked, see Fig. 2), it can be effectively represented by a maximum of four dimensions. This theoretical result was confirmed by the data. The importance for learning is that deviations form the 'ideal' juggling pattern lead to an increased dimensionality of the system.

1.3 Postural sway and supra-postural performance

The time structure of postural sway, as present in the CoP-trajectories, strongly depends on the context in which it is generated. For instance, CoP-trajectories obtained during quiet standing are characterized by a random-like time evolution (Collins and De Luca 1993; Frank et al. 2000; Newell at al. 1997; and Riley 2001 for a recent overview), which prompted researchers to opt for various forms of stochastic process modeling. Similar time structures have been observed in CoP-trajectories obtained during the performance of a supra-postural aiming task (Balasubramaniam et al. 2000). In contrast, if subjects are requested to visually track a periodically moving stimulus, then body sway (operationalized as head motion and hip and ankle rotation) exhibits stimulus-correlated periodic motion (Bardy et al. 1999; Marin et al. 1999). Presumably, the main periodic properties of body sway in the latter studies would, at least to a certain extent, also show up in the CoP-trajectories, if they would have been measured. Collectively, these observations suggest that postural sway may become organized in qualitatively different, task-specific ways.

1.4 Locomotor-respiratory coupling

Locomotor-respiratory coupling (LRC) has been found in a variety of locomotor activities, including running, rowing, cycling and manual wheelchair propulsion (see, e.g., Amazeen et al. 2001; Bernasconi and Kohl 1993; Mahler et al. 1991; Paterson et al. 1986; Takano 1995). In general, a variety of coupling ratios between locomotion and breathing has been observed. For instance, rowers take one, two or three breaths within a full stroke. Moreover, the coupling is often intermittent, and individuals are not always consistent with regard to the adopted coupling ratios (Siegmund et al. 1999). These findings suggest that respiration is weakly, or flexibly, coupled to locomotion. However, both coupling strength and the number of coupling modes has been shown to increase with practice (Mahler et al. 1991). This is also apparent from comparisons between well-trained and untrained subjects (Amazeen et al. 2001; Bramble and Carrier 1983; Mahler et al. 1991).

Two causes of LRC have been put forward. First, it has been widely suggested that LRC is brought about by mechanical deformations of the thorax and the diaphragm, with the so-called visceral piston hypothesis for walking as the most concrete example (Bramble 1986; Bramble and Carrier 1983). Second, it has been argued that LRC is a function of aerobic demands, because oxygen consumption has been shown to be lower during periods of entrainment than during non-entrainment in bicycle ergometry (Garlando et al. 1985). An alternative explanation has recently been proposed by Amazeen et al. (2001), who investigated the emergence of coupling modes during manual wheelchair propulsion as a function of power output and movement frequency. Increasing movement frequency altered the adoption of specific frequency ratios that are well documented in the motor coordination literature. This observation, in combination with the recognition that mechanical loading of the diaphragm is small in wheelchair propulsion, led the authors to argue that LRC may be understood in terms of 'informationally' coupled non-linear oscillators.

1.5 Experimental expectations

The experiment reported here was conducted to verify the validity of three expectations. First, in line with numerous skill acquisition studies, we expected task performance to improve asymptotically. For the activity of interest, cascade juggling, task performance may be conveniently quantified in terms of the degree of satisfaction of the prevailing task constraints. Second, in spite of the highly variable and erratic nature of CoP-trajectories during normal quiet stance (resulting in broad band spectral densities), we expected the repetitive, manually induced perturbations of the CoP-components to manifest themselves and to evolve into distinct components in the spectral estimates. That is, we expected the arm movements to become functionally embedded in the orthogonal components of the CoP, resulting in task-specific patterns of frequency locking with the ball movements. Third, in view of the previously summarized literature and considering the small mechanical deformations of the thorax and diaphragm and the low aerobic demands in juggling, we expected distinct patterns of frequency locking between ball and respiration cycles to occur, which would provide strong support for the postulated role of coordinative rather than purely biomechanical principles in the emergence of motor-respiration couplings in general.

2 Method

2.1 Subjects

Six students (5 female, 1 male) participated in the experiment after having given their informed consent.

Their ages varied between 20 and 23 years (mean 21.7 years). All subjects had normal (or corrected to normal) vision and no prior juggling experience. One (female) subject was left-handed. The subjects were paid for their participation.

2.2 Procedure

During a four-week period the subjects practiced the 3-ball cascade juggle during twenty one-hour sessions (five daily sessions per week). Practice outside the sessions was not allowed. On the 2nd, 5th, 8th, 11th, 14th, 17th and 20th day, the session was ended with a three minute lasting recording trial in which subjects were instructed to juggle as steadily and as long as possible. In the case of eventual failures subjects were invited to start over again. Each successful juggle was stored as individual time series. This procedure resulted in varying numbers of time series of different lengths for successive days. In view of the reliability and accuracy of the analyses to be performed, trials were excluded if they did not contain at least 8 consecutive throws for each ball (i.e., 24 consecutive throws in total).

2.3 Apparatus

Each experimental trial was video-taped and, subsequently, the displacements of the balls in the horizontal and vertical direction were digitized (WinAnalyse, Mikromak). The floor-mounted camera (sampling frequency 50 Hz per half-frame) was placed 3.20 m in front of the subjects. Both the experimental and the practice sessions were performed with three plastic 'stage balls' with a diameter of 7.3 cm and a mass of 130 g.

Subjects were standing on a one-by-one meter force platform (sampling frequency 200 Hz), which measured the ground reaction forces by means of eight strain gauges (four in the vertical and four in the horizontal direction). These force signals were amplified (SCXI-1121 Amplifiers, National Instruments) and subsequently stored on a computer for off-line data analysis. The force platform was calibrated before each experimental session. To simultaneously measure respiration, the subjects wore a helmet to which a pneumotachometer was attached (see Fig. 1). The sampling frequency of the pneumotachometer was 200 Hz. Synchronization of the video, force platform and respiration recordings was achieved by means of a time-code generator.

2.4 Pre-processing

From the eight time series of the ground reaction forces both CoP-components, i.e., anterior-posterior (AP) and medio-lateral (ML) sway, were computed. To eliminate transients, the first full juggling cycle was removed from all time series. Furthermore, the length of the time series was adjusted to integer periods of the ball trajectories to improve the reliability of the spectral estimates. Consequently, the time series of the first ball started and ended with equal phasing. All other time series were aligned accordingly. The trajectories of the ball movements were further interpolated by means of cubic splines to obtain an effective sampling frequency of 200 Hz. As a result, all the time series were equally sampled.

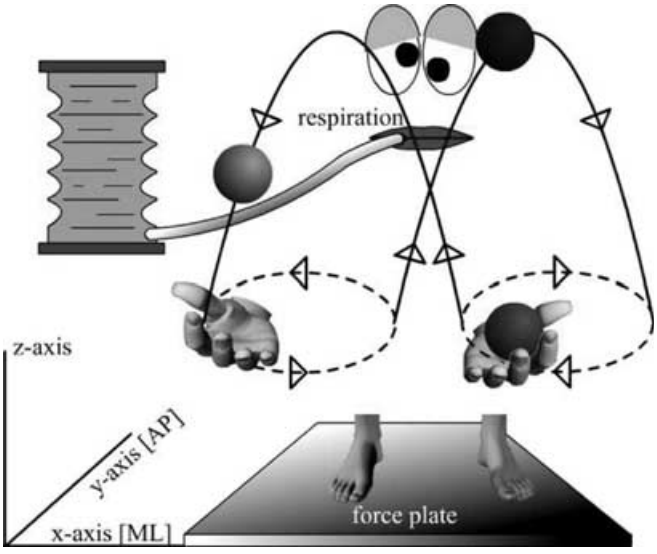

Fig. 1. Experimental set-up (see text)

2.5 Discrete methods

The temporal and spatial locations of the throws and catches were estimated by exploiting the fact that the ball trajectories in free flight obey the laws of ballistic motion. That is, once the ball leaves the hand it maintains a (nearly) constant horizontal velocity while a parabola characterizes the vertical displacement. After having determined the locations of the zeniths of the ball flights, we fitted the ball trajectories to a parabola and defined the locations of throws and catches as the points at which the relative deviation from that parabola was larger than 5% (Post et al., 2000).

Obviously, functionally distinct temporal locations in the ball trajectories are the moments at which the balls leave or enter the hands. Recognizing that the hand cycle time could be either defined as the time interval between consecutive throws or between consecutive catches by the same hand, we computed the temporal distance both between consecutive throws (Δt_T) and between consecutive catches (Δt_C).

The spatial extent of the juggling pattern and its variability were examined by calculating the distances between left hand throws (or catches) and subsequent right hand throws (or catches); H_T^{balls}: horizontal distance throws; V_T^{balls}: vertical distance throws; H_C^{balls}: horizontal distance catches; V_C^{balls}: vertical distance catches. In addition to these measures, which all pertain

to the ball trajectories, we focused on the reproducibility or steadiness of the hand location at the moments of catching and throwing. For this purpose, the distances between consecutive throws (or catches) of the same hand were calculated; see Fig. 2 (H_T^{hand} throws in horizontal direction; V_T^{hand}: throws in vertical direction; H_C^{hand}: catches in horizontal direction; V_C^{hand}: catches in vertical direction).

In order to minimize the influence of the different intersubject tempi of performance on the outcome of the analyses, we rescaled all dependent variables (i.e., Δt_T, H_T^{balls}, etc.) for each individual subject to their smallest intratrial mean in the entire experiment, which was arbitrarily set at 100. For all the temporal and spatial variables the intratrial means and coefficients of variation (CV) were computed.

Subsequently, we looked for eventual changes in error correction mechanisms in the course of learning (Post et al. 2000; Wing and Kristofferson 1973). Lag-one and -two auto-correlations between consecutive throws and between consecutive catches of the same hand (i.e., left, right) were determined in both the temporal and spatial domain. Further, lag-one cross-correlations were calculated between the temporal variables and both the horizontal and vertical spatial components of consecutive catches, as well as consecutive throws, of the same hand. Finally, we computed lag-one cross-correlations between the horizontal and vertical spatial components of both consecutive catches and throws.

2.6 Continuous methods

All the variables introduced thus far exclusively provide information about distinct points in the juggling patterns produced. Although these points are likely to be rather informative, their choice is to some degree arbitrary. Eventual intermediate (i.e., time-continuous) effects, which, for instance, may give rise to the occurrence of certain cross-correlations, remain unaddressed in such a coarse-grained analysis. Indeed, for posture and respiration it is difficult, if at all possible, to identify similarly straightforward distinct points as in the juggling patterns – hence, we did not subject the corresponding time series to any discrete analyses. Instead, to study possible relations between the subsystems of interest, that is, ball movements, stance and respiration, we analyzed all time series using both time-continuous measures and time-integrating analyses.

2.6.1 Frequency locking. As the trials contained different numbers of samples resulting in different frequency resolutions, we applied a zero-padding to create time series of equal length for each trial. All power spectral densities $P(\omega)$ were estimated by applying Welch's periodigram method (e.g., Stoica and Moses 1997) and normalized to time series with unit variance (thus rendering all the results pertaining to the spectral analysis dimensionless). The main frequency, ω_0, was identified as the peak containing the most spectral power. With respect

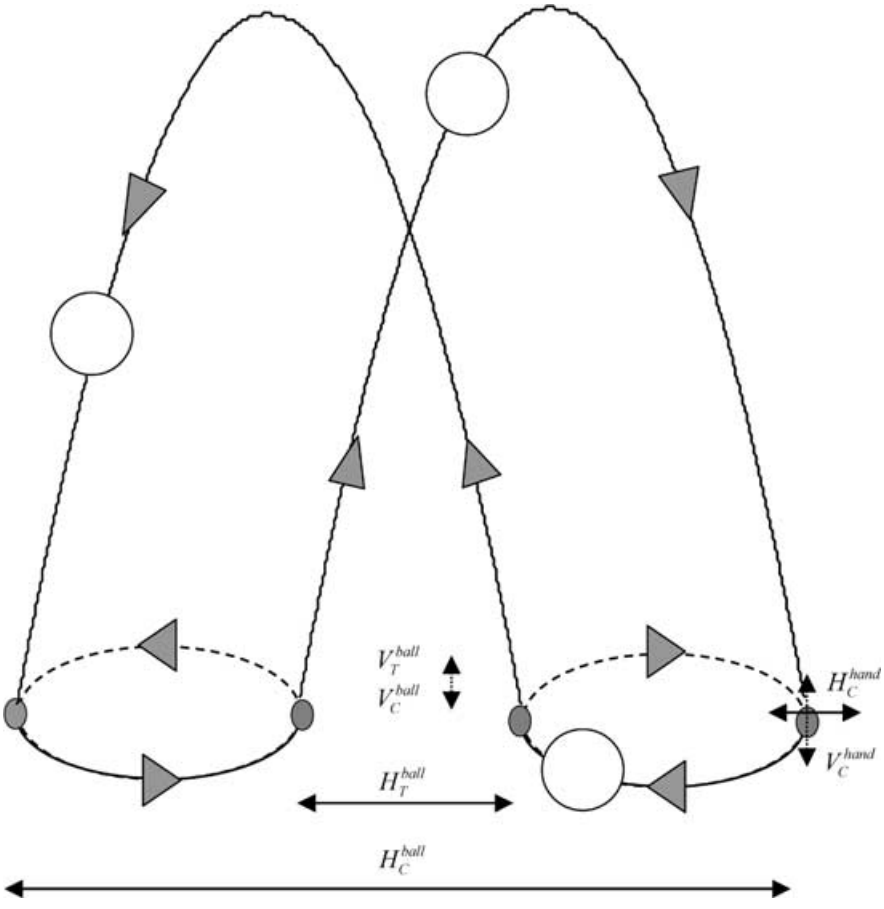

Fig. 2. Schematic representation of the standard cascade. The position of the throws is represented by the *inner gray ellipses*, the position of the catches by the *outer gray ellipses*. The dependent discrete spatial variables are highlighted (see text)

to this main frequency, the amount of spectral power at the first sub-harmonic ($\omega_{sub} = \omega_0/2$) as well as at the first two (super-)harmonics ($\omega_1 = 2\omega_0$ and $\omega_2 = 3\omega_0$) were determined. Eventual cross-links between different time series were further quantified through the relation between the dominant frequencies of different time series. In all the analyses, we chose the frequency of the vertical ball trajectory as reference[1] and computed its ratio relative to the frequencies of the horizontal ball movements, AP- and ML-sway, and respiration. A $p:q$ frequency locking between time series of different activities was considered to be present if

$$\frac{(p\cdot\omega_{0,x}-\Delta\omega)}{(q\cdot\omega_{0,y}+\Delta\omega)}\leq\frac{\omega_{0,x}}{\omega_{0,y}}\leq\frac{(p\cdot\omega_{0,x}+\Delta\omega)}{(q\cdot\omega_{0,y}-\Delta\omega)}$$

where $\omega_{0,x}$ and $\omega_{0,y}$ denote the main frequencies of general time series $x(t)$ and $y(t)$, respectively, and $\Delta\omega$ is the frequency resolution of the corresponding spectral estimates. For each trial, the strength of frequency locking between the time series was operationalized by means of

$$\psi_{x,y}(\rho)=2N\frac{\int P_x(\omega)\cdot P_y(\rho\cdot\omega)\mathrm{d}\omega}{\int[P_x^2(\omega)+P_y^2(\rho\cdot\omega)]\mathrm{d}\omega}$$

where P_x and P_y represent the spectral densities of the time series $x(t)$ and $y(t)$. Notice that the integration only includes the frequency interval up to the smallest Nyquist frequency, that is, the actual sample frequency of the video-recordings, i.e., 25 Hz; N is a normalization factor[2] defined as $8N^2=(\rho^2+1)/(\rho+1)$. The ratio ρ was always fixed at the value of the trial's frequency locking ratio p:q, determined as stated above. The stronger the similarity between two spectra after an appropriate rescaling ρ of the frequency axis, the larger their overlap and thus the higher the value of $\psi_{x,y}(\rho)$ (see Daffertshofer et al. 2000).

2.6.2 Relative phasing. To address the time-dependent relative phasing between two time series $x(t)$ and $y(t)$ we utilized the Hilbert phase based on analytic signals. This approach was preferred as it unambiguously provides the instantaneous phase and amplitude for an arbitrary signal. In brief, as complex extension of a real time series $s(t)$, the analytic signal $\zeta(t)=s(t)+i\cdot u(t)$ can be uniquely defined via the Hilbert transform (Gabor 1946)

$$u(t)=\frac{1}{\pi}PV\int_{-\infty}^{\infty}\frac{s(\tau)}{t-\tau}\mathrm{d}\tau$$

in which PV refers to the Cauchy principal value. As for every complex-valued quantity, one can introduce amplitude and phase in terms of $\zeta(t)=A(t)\cdot\exp\{i\cdot\Theta_H(t)\}$. In other words, $\Theta_H(t)=\arctan[\Im\{\zeta(t)\}/\Re\{\zeta(t)\}]=\arctan[u(t)/s(t)]$ defines the continuous (Hilbert) phase of the time series $s(t)$. The relative phase $\Delta\Theta_H(t)$ between two time series $x(t)$ and $y(t)$ is then defined as $\Delta\Theta_H(t)=\Theta_{H,y}(t)-\Theta_{H,x}(t)$ (see, e.g., Pikovsky et al. 1997, and references therein). For our purposes, we need to generalize the latter definition in terms of $\Delta\Theta_H(t)=p\Theta_{H,y}(t)-q\Theta_{H,x}(t)$ as we are interested in cases of $p:q$ frequency locking. For all the trials in which frequency locking was observed, both the mean and the variance of the corresponding relative phases were computed in terms of circular statistics. In addition, the amount of spectral power in the first sub- and super-harmonics (ω_{sub} and ω_1,ω_2) was determined. The frequency locking strength and the variance of the relative Hilbert phase were subjected to statistical analyses (paired t-tests) and regression, just as was done for the discrete variables.

2.6.3 Cross-covariance. The spectral analyses revealed small but significant changes in the ball trajectories as a function of learning, as well as changes of a qualitative nature in the CoP-dynamics – this will become more apparent in the *Results* section. The structure of the latter, however, was unclear. Hence, the data were further subjected to cross-covariance analyses, in particular, principal component analysis (PCA) in order to pinpoint the explicit composition of the two CoP-components in relation to juggling performance. The PCA is based on the diagonalization of the covariance matrix, that is, one extracts eigenvalues that are interpreted as variances of the entire time series in question. In the present study, however, we attempted to extract dynamical changes in the course of learning. Note that integrative measures like the covariance structure are not necessarily informative in this regard. We therefore introduced a (discrete) time-dependency by means of a 'windowed' PCA[3]: for each particular activity a 5D space or 'window' was constructed by combining five consecutive trials into a state vector, $\boldsymbol{s}(t)=[s_1(t),s_2(t),s_3(t),s_4(t),s_5(t)]^{\mathrm{T}}$. This window was moved through the successive trials, with the first state vector containing trials 1 to 5, the second trials 2 to 6, and so on. Each of the so-generated 5D systems was subjected to a separate PCA, followed by an analysis of the convergence of the resulting eigenvalues and the structures of the time series projected onto the corresponding eigenvectors.

2.7 Learning

The present data did not allow for the application of conventional statistical methods such as analyses

[1] All the analyses with respect to frequency locking ratio and the strength thereof were performed on the vertical ball trajectories because the number of cycles in this direction is twice as large than in the horizontal direction, yielding a better numerical accuracy.

[2] The normalization factor N corrects for the systematic deformation of the spectral estimate P_y due to the stretching of the frequency axis as a function of ρ, implying a change of the line element $\mathrm{d}\omega$.

[3] We first subjected the data to a conventional PCA before applying the window technique. In our view, the latter method is superior in revealing changes in the structure of both sway components, which was our objective. Thus, only the results obtained with the windowed PCA are presented. Note that in order to be able to optimally compare trials, all the time series were first resampled so as to match the main frequency of the vertical ball evolutions in the slowest trial.

of variance (ANOVA's) due to differences in the number of trials between subjects/days. To cope with this problem, we applied two alternative techniques providing (necessarily crude) impressions of the learning process. First, for each subject, we computed the means of all dependent variables for the trials performed at the first day (defined as the day at which the juggle had been successfully performed for the first time) and the trials performed at the last day. The so-obtained trial-means were subjected to two-tailed paired *t*-tests. Clearly, this procedure only allows for a statistical comparison between initial and final learning phases; it provides no fine-grained information about the learning dynamics. At second, we therefore performed a nonlinear regression analysis of the 'learning curves' of all dependent variables as comprised by their session means. Specifically, a simplex minimization procedure was employed (Nelder and Mead 1965), utilizing the least squares between the variable of interest and the function $A-B\mathrm{e}^{-\lambda t}$. Recall that this function can account for exponentially up to (nearly) linearly increasing as well as for decreasing 'learning curves', depending on the values of A, B and λ, and that $\tau = 1/\lambda$ can be interpreted as the characteristic learning time.

Since in some subjects the evolution of some dependent variables was sometimes too irregular to allow for a reliable regression only those time series were included whose R^2 had exceeded 50% and whose values of λ was found within the interval given by twice the standard deviation around the median.[4] Consequently, group means were calculated if for at least four out of six subjects both these criteria were met.

3 Results

3.1 Ball movements

Table 1 summarizes the results of the statistical analyses that were performed on the temporal variables. Note that the function $A-B\mathrm{e}^{-\lambda t}$ decreases if $B < 0$ and increases if $B > 0$ for $\lambda > 0$. On average, the temporal distances between all consecutive points decreased in the course of the experiment, indicating that juggling tempo increased with practice. The intervals between consecutive throws (Δt_T) and between consecutive catches (Δt_C) changed on approximately the same time-scale, i.e., $\lambda_{\Delta t_\mathrm{T}} \approx \lambda_{\Delta t_\mathrm{C}}$. The increase in speed was accompanied by a decrease in variability of all temporal variables considered. The most pronounced effect was found for the temporal locations of the catches whose coefficient of variation ($\mathrm{CV}\Delta t_\mathrm{C}$) dropped to the same order of magnitude as that of the temporal locations of the throws ($\mathrm{CV}\Delta t_\mathrm{T}$). The latter remained roughly constant ($\lambda_{CV\Delta t_\mathrm{T}} \approx 0$), whereas $\mathrm{CV}\Delta t_\mathrm{C}$ decreased rather quickly according to $\lambda_{CV\Delta t_\mathrm{C}} \approx 0.26\mathrm{d}^{-1}$, that is, with a characteristic time of $\tau_{CV\Delta t_\mathrm{C}} = 1/\lambda_{CV\Delta t_\mathrm{C}} \approx 3.8$ d (= days). The characteristic times were quite variable across subjects so that their mean values reported in Table 1 should be viewed more as indicators of orders of magnitude rather than as representative for the individual performances.

Table 1. Means of the paired *t*-tests as well as the λ and R^2 values of the regression on the intratrial mean values ($\langle\cdot\rangle$) and intratrial coefficients of variation (CV ·) of the discrete (normalized) temporal variables. A '*' (after the means of the last day) indicates that statistical significance of the paired *t*-tests was reached at $p < 0.05$ level, while a '**' indicates a significance level of $p < 0.10$. The superscript denotes the number of subjects included in the calculation of the group mean and standard deviation regarding the parameters of the regression analysis

	⟨first day⟩	⟨last day⟩	λ	R^2
$\langle\Delta t_\mathrm{T}\rangle$	130 ± 19	$106 \pm 6^{**}$	$0.21 \pm 0.28^{(4)}$	0.96 ± 0.04
$\mathrm{CV}\Delta t_\mathrm{T}$	12 ± 2	10 ± 2	$0.08 \pm 0.16^{(5)}$	0.80 ± 0.14
$\langle\Delta t_\mathrm{C}\rangle$	129 ± 19	$106 \pm 6^{**}$	$0.21 \pm 0.28^{(4)}$	0.95 ± 0.05
$\mathrm{CV}\Delta t_\mathrm{C}$	22 ± 6	$12 \pm 3^{*}$	$0.26 \pm 0.23^{(5)}$	0.94 ± 0.11

Corresponding results for the spatial variables are shown in Table 2. In general, the CV of the spatial variables pertaining to the ball movements ($H_\mathrm{T}^\mathrm{ball}, H_\mathrm{C}^\mathrm{ball}, V_\mathrm{T}^\mathrm{ball}, V_\mathrm{C}^\mathrm{ball}$) were smaller than those pertaining to the hand movements ($H_\mathrm{T}^\mathrm{hand}, H_\mathrm{C}^\mathrm{hand}, V_\mathrm{T}^\mathrm{hand}, V_\mathrm{C}^\mathrm{hand}$). This is consistent with Van Santvoord and Beek's (1996) conclusion that the focus of control in juggling is directed predominantly at events associated with the ball movements rather than the hand movements. In the present study, the effect was more pronounced in the vertical than in the horizontal direction, particularly at the last day. In view of this insight into the locus of control, we expected that the effects of learning in the present study would be associated more with the ball movements than

Table 2. Means of the paired *t*-tests as well as the λ and R^2 values of the regression on the intratrial mean values ($\langle\cdot\rangle$) and intratrial coefficients of variation (CV ·) of the discrete (normalized) spatial variables. See Table 1 for an explanation of the asterisks and the superscripts

	⟨first day⟩	⟨last day⟩	λ	R^2
$\langle H_\mathrm{T}^\mathrm{ball}\rangle$	334 ± 290	142 ± 20	$-0.13 \pm 0.44^{(5)}$	0.82 ± 0.14
$\mathrm{CV}H_\mathrm{T}^\mathrm{ball}$	65 ± 5.6	$45 \pm 6.5^{*}$	$0.09 \pm 0.10^{(5)}$	0.86 ± 0.17
$\langle H_\mathrm{C}^\mathrm{ball}\rangle$	156 ± 42	124 ± 9	–	–
$\mathrm{CV}H_\mathrm{C}^\mathrm{ball}$	74 ± 9	71 ± 3	–	–
$\langle V_\mathrm{T}^\mathrm{ball}\rangle$	576 ± 264	424 ± 199	–	0.82 ± 0.14
$\mathrm{CV}V_\mathrm{T}^\mathrm{ball}$	44 ± 13	$23 \pm 4^{*}$	$0.40 \pm 0.38^{(5)}$	
$\langle V_\mathrm{C}^\mathrm{ball}\rangle$	311 ± 232	252 ± 180	$0.61 \pm 0.18^{(5)}$	0.96 ± 0.03
$\mathrm{CV}V_\mathrm{C}^\mathrm{ball}$	71 ± 18	$48 \pm 10^{*}$	$0.18 \pm 0.22^{(5)}$	0.82 ± 0.18
$\langle H_\mathrm{T}^\mathrm{hand}\rangle$	320 ± 74	$156 \pm 32^{**}$	$-0.04 \pm 0.53^{(5)}$	0.88 ± 0.17
$\mathrm{CV}H_\mathrm{T}^\mathrm{hand}$	73 ± 10	73 ± 7	–	
$\langle H_\mathrm{C}^\mathrm{hand}\rangle$	249 ± 82	$139 \pm 10^{*}$	$0.07 \pm 0.07^{(5)}$	0.85 ± 0.14
$\mathrm{CV}H_\mathrm{C}^\mathrm{hand}$	73 ± 8	76 ± 3	–	
$\langle V_\mathrm{T}^\mathrm{hand}\rangle$	442 ± 196	$184 \pm 53^{*}$	$0.19 \pm 0.22^{(5)}$	0.93 ± 0.07
$\mathrm{CV}V_\mathrm{T}^\mathrm{hand}$	118 ± 21	118 ± 18	–	
$\langle V_\mathrm{C}^\mathrm{hand}\rangle$	382 ± 283	$152 \pm 21^{**}$	$0.30 \pm 0.23^{(5)}$	0.93 ± 0.12
$\mathrm{CV}V_\mathrm{C}^\mathrm{hand}$	88 ± 22	81 ± 2.9	–	

[4] Given the large number of variables (30) one could not expect to find a reliable fit for all the regressed time series in terms of a single equation. However, 22 variables allowed for rather accurate regressions (see also *Results*, Sect. 3). Hence, we chose not to increase the number of regression equations as our aim was to capture the overall learning pattern.

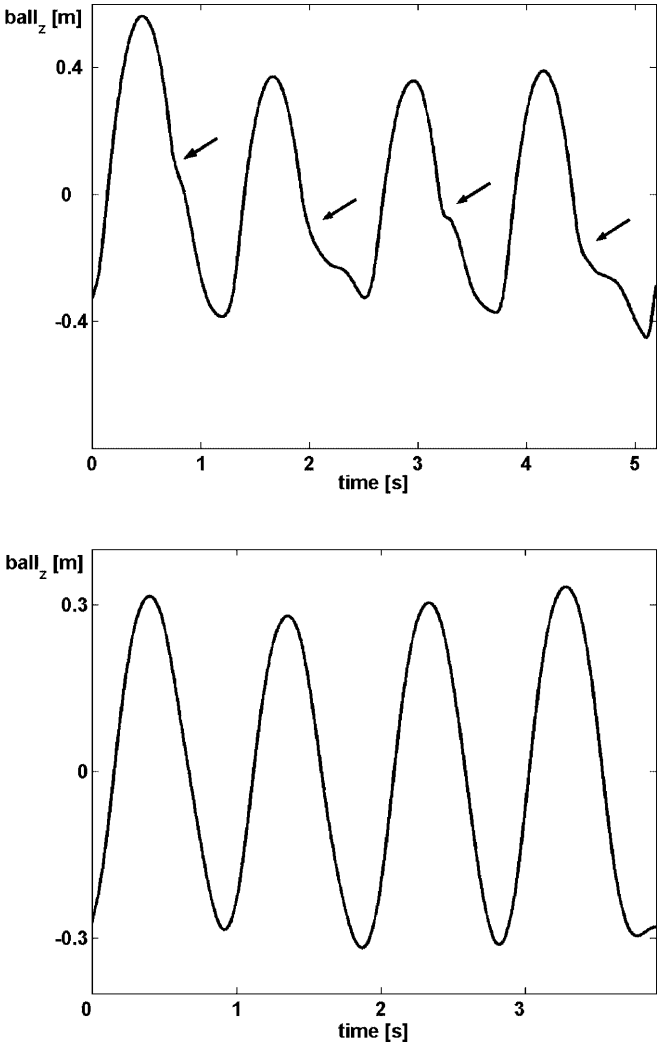

Fig. 3. Comparison of the time series of a vertical ball trajectory ($ball_z$) of a trial at the first day (*upper plot*) and at the last day (*lower plot*). Jagged trajectories due to the catches (indicated by the *arrows*) become smoother (i.e., less jagged) with practice (last day), indicating that the hands' movements had become adjusted to the balls' movements at the moment of catching

with the hand movements. Indeed, the variability of the ball movements decreased significantly by a factor up to two (Table 2: H_C^{ball}, V_T^{ball}, V_C^{ball}, and H_T^{ball}), whereas the (rescaled) variability of the hand movements (H_T^{hand}, H_C^{hand}, V_T^{hand}, and V_C^{hand}) remained approximately constant. Since the means of the latter variables decreased, it may be deduced that in absolute terms, their variability became smaller. The clear-cut results presented thus far notwithstanding, the present study did not always result in consistent learning curves. Indeed the overall variability of the throw/catch positions was fairly high rendering fitting procedures unreliable and, hence, the fit parameters showed a rather high inter-subject variability.

For the time-continuous temporal measures we found that in the vertical direction the spectral power accounted for by the super-harmonics ω_1 and ω_2 decreased significantly in the course of learning, indicating that juggling

Table 3. Means of the paired *t*-tests as well as the λ and R^2 values of the regression on the intratrial mean values of the harmonics (ω), the frequency locking strengths (ψ) and the variance of the relative Hilbert phases ($\sigma\Delta\Theta_H$) between the ball trajectories (*bx* and *bz* refer to trajectories in horizontal and vertical direction, respectively). See Table 1 for an explanation of the asterisks and the superscripts. Note that a positive sign of B is indicated by $^{(+)}$ in front of the values of λ

	⟨first day⟩ ($\times 10^{-3}$)	⟨last day⟩ ($\times 10^{-3}$)	λ	R^2
$\omega_{sub}(bx)$	5.18±3.79	2.67±1.06*	–	–
$\omega_1(bx)$	2.38±0.48	0.48±0.30*	0.38±0.29$^{(5)}$	0.84±0.20
$\omega_2(bx)$	0.97±1.17	1.17±1.17	$^{(+)}$0.15±0.12$^{(5)}$	0.84±0.12
$\omega_{sub}(bz)$	1.19±1.22	0.85±0.54	0.74±0.31$^{(5)}$	0.81±0.11
$\omega_1(bz)$	3.25±2.56	0.33±0.24*	0.25±0.20$^{(6)}$	0.98±0.02
$\omega_2(bz)$	0.35±0.31	0.15±0.09*	0.25±0.14$^{(5)}$	0.83±0.12
$\psi bx, bx$	980.2±27.75	996.1±3.25*	$^{(+)}$0.26±0.24$^{(4)}$	0.84±0.20
$\psi bz, bz$	996.1±3.41	999.3±0.46*	$^{(+)}$0.31±0.21$^{(5)}$	0.94±0.06
$\sigma\Delta\Theta_{H(bx,bx)}$	111.4±100.8	61.94±22.03*	0.29±0.17$^{(4)}$	0.96±0.04
$\sigma\Delta\Theta_{H(bz,bz)}$	97.58±30.32	32.85±5.35*	0.22±0.19$^{(6)}$	0.97±0.04

performance became smoother (see Fig. 3). In contrast, in the horizontal direction the spectral power contained in ω_1 and in the subharmonics ω_{sub} decreased significantly, whereas the spectral power in ω_2 increased, albeit not significantly due to the high between-subject variability (for a summary of this harmonic analysis, see Table 3).

As expected, in all trials a 1:1 frequency locking was observed between paired ball trajectories, that is, ball 1 $\leftrightarrow$ 2, ball 1 $\leftrightarrow$ 3, and ball 2 $\leftrightarrow$ 3, in both spatial directions. Inevitably, each ball trajectory showed a 1:2 frequency locking between its horizontal and vertical component. The strength of these frequency locks increased significantly in the course of learning. Paired *t*-tests showed that in both directions the variance of the relative Hilbert phase between the frequency-locked ball trajectories decreased significantly, indicating an increasing precision of the timing of the balls' circulation. In general, all time-continuous measures evolved with $\lambda > 0$, that is, they saturated exponentially as shown in Fig. 4.

In line with the results of the harmonic analysis, that is, the increasing smoothness of juggling performance, variability decreased and, likewise, stability increased asymptotically, according to both cross-spectral estimates and the relative phasing between the ball movements (see Table 3).

Finally, the auto-correlation analysis carried out for the temporal variables revealed that the lag-one auto-correlation of the catch intervals was significantly negative [$t(136) = -7.888$, $p < 0.001$], whereas the lag-two auto-correlations vanished.[5] This suggests that eventual errors in the timing of the catches were corrected immediately, that is, at the next catch. An equivalent timing

[5] Note that in this analysis, the results of the correlation analysis for each single trial of all subjects were first collapsed and then statistically tested to obtain a global impression of each variable's correlation structure over the entire experiment. This step was deemed justified because no changes in the correlation structures were found as a function of practice.

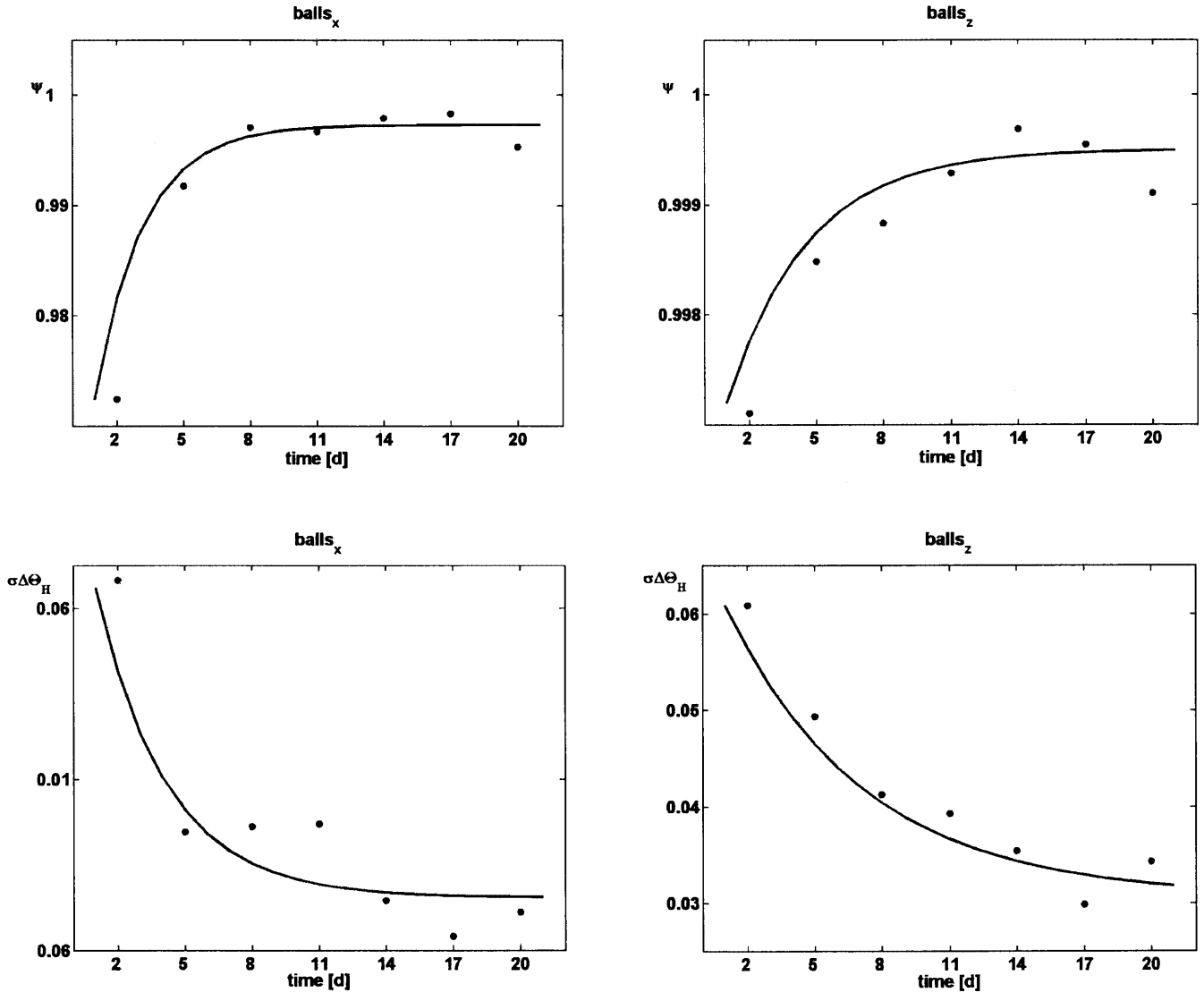

Fig. 4. Exponential fit of the evolution of the frequency locking strength (Ψ) and variance of the relative Hilbert phase ($\sigma\Delta\Theta_H$) between ball trajectories in horizontal and vertical directions for one subject; *upper left* and *upper right panel* and *lower left* and *lower right panel*, respectively

correction for the throw points could not be established. A similar error correction was found in the spatial components. In addition to negative lag-one auto-correlations for $H_C^{ball}, V_T^{ball}, V_C^{ball}$, and H_T^{ball} [$t(136) = -23.37$, $p < 0.001$, $t(136) = -28.08$, $p < 0.001$, $t(136) = -19.00$, $p < 0.001$, $t(136) = -22.71$, $p < 0.001$, respectively]; we also found (small) negative lag-two autocorrelations ($t(136) = -3.75$, $p < 0.001$, $t(136) = 2.16$, $p = 0.016$, $t(136) = -10.23$, $p < 0.001$, $t(136) = -2.90$, $p < 0.002$), suggesting that spatial error corrections may be postponed, at least to a degree. Apparently, in cascade juggling the spatial components are less constrained than the temporal components. In brief, both the temporal and spatial variability of performance decreased in the course of learning. This reduction was observed for variables associated with both ball and hand movements. In the latter case, however, the reduction was confined to the decrease of movement amplitude.

3.2 Correlation between ball movements and center-of-pressure

The dynamical properties of postural sway were quite variable both within and between subjects, as can be appreciated from Fig. 5. In the upper left panel of this figure, one can also find an emergence of spectral components around 3 Hz corresponding to 1:3 frequency locking (see also below), while in the upper right panel one can observe spectral components around 1.5 Hz which point at the presence of 2:3 frequency locking (see below). Spectral analyses revealed that ML- and AP-sway were sometimes frequency locked to the vertical component of the ball trajectories. Because frequency locking between the horizontal and vertical direction of the ball movements was always present, CoP locking with the vertical ball trajectory implies an equivalent locking, albeit with half its ratio, in the horizontal direction. Specifically,

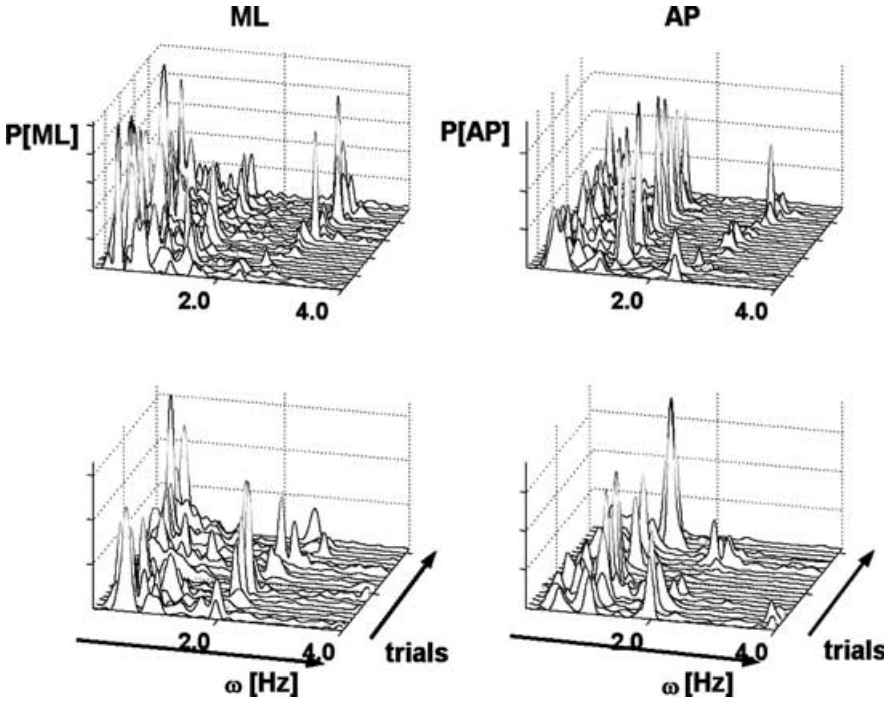

Fig. 5. Power spectral densities for ML- and AP-sway (*left* and *right column*, respectively) as a function of practice (trials) for two subjects (two rows)

averaged over all trials, that is, over all subjects and all days, the following locking ratios were observed:

2:3 (51% for AP-sway, 3% for ML-sway);
1:3 (13% for AP-sway, 27% for ML-sway);
2:1 (1% for AP-sway, 6% for ML-sway).

Recall that as a single ball oscillates once in the vertical direction, the other two balls do so as well, thus corresponding to three arm oscillations. A 2:3 frequency locking ratio thus signifies that one sway cycle is completed as both arms oscillate once. Similarly, a 1:3 locking ratio signifies that one sway cycle is passed through while a single arm oscillates once. The 2:3 locking ratio for ML-sway disappeared completely after the 11th day (in 64% of the trials no locking was present). As regards AP-sway, the incidence of the 2:3 locking ratio slightly increased with practice, whereas the incidence of the 1:3 locking ratio decreased (in 35% of all trials no frequency locking occurred). The evolutions of the locking strength were too variable and the variance of the relative phase were too large to allow for meaningful regression analyses, which were therefore omitted.

The subsequent analyses were based on the windowed PCA explained in the *Method* section. These analyses confirmed the previously obtained results regarding the changes in the spectral distribution and strength of frequency locking for the ball trajectories. Moreover, the windowed PCA allowed for an assessment of the manner in which the principal components as extracted from the various time-series changed in the course of the experiment. Particularly, the results pertaining to changes in the coordination between the sway components and the ball trajectories were illuminating in this regard. Throughout the experiment, 2:1, 2:3, and 1:3 frequency locking ratios were observed between the projection onto the first mode of the vertical component of the ball trajectories and the projections onto the most prominent modes of ML-sway[6] (see Fig. 6). Note that, the projections onto the most prominent modes cover the main, but not all, variance of the time series in a certain window (see also *Method section 2.6.3* and compare Fig. 6 with Fig. 5; the former clearly reveals more structure than the latter). For four subjects, the largest peak of the spectral power density of the projections onto the first (or sometimes even the second) mode of the ML-sway shifted in the course of learning. In two of those four subjects (s4, s6) this 1:3 frequency locking was preserved throughout the experiment once it had become dominant, whereas in the other two subjects (s2, s3) it gradually resolved into unlocked states as the low frequency components became dominant. For the other two subjects (s1, s5) the amount of spectral power defining the 1:3 frequency locking increased but either never became dominant or remained dominant from the first day onward.

As for ML-sway, 2:1, 2:3, and 1:3 frequency locking ratios between the vertical component of the ball trajectories and the projections onto the most prominent modes of AP-sway were observed (see Fig. 7, cf. Fig. 5). Three subjects (s4, s5, s6) revealed changes in frequency locking ratio during learning in that the spectral peak of the projection corresponding to the 2:3 mode became most dominant – note that for s5, initial dominance of

[6] Both spectral analyses and PCA revealed a 2:1 frequency locking between the vertical ball trajectories and the CoP-components. In this analysis, however, the particular CoP-frequencies were embedded in a broad band of low frequencies that could not be related to juggling performance (in the frontal plane). Thus, we attributed these components to slow fluctuations rather than to a functional coupling.

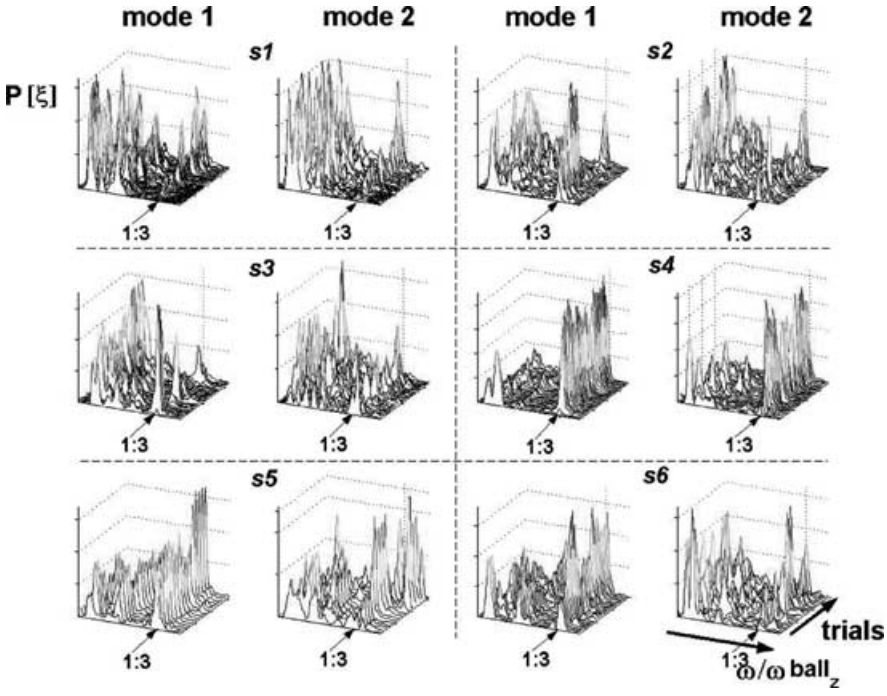

Fig. 6. Power spectral densities ($P[\xi]$) of the projections onto the first two modes of ML-sway for the windowed PCA as a function of practice for each subject (s1… s6). For each subject the spectral density estimates of the first mode is displayed on the left-hand side of the subject denotation and the second mode on the right-hand side. The *thin arrow* on the frequency axis ($\omega/\omega_{\mathrm{ball}_z}$) in each single panel indicates the frequency which corresponds to a 1:3 locking ratio between the ball movements in the vertical direction and ML-sway. The *thick arrow* (*lower right panel*) indicates practice time (in trials). To exemplify, the *upper left panel* reveals an increase of the spectral component of the projection onto the first mode corresponding to a 1:3 frequency locking

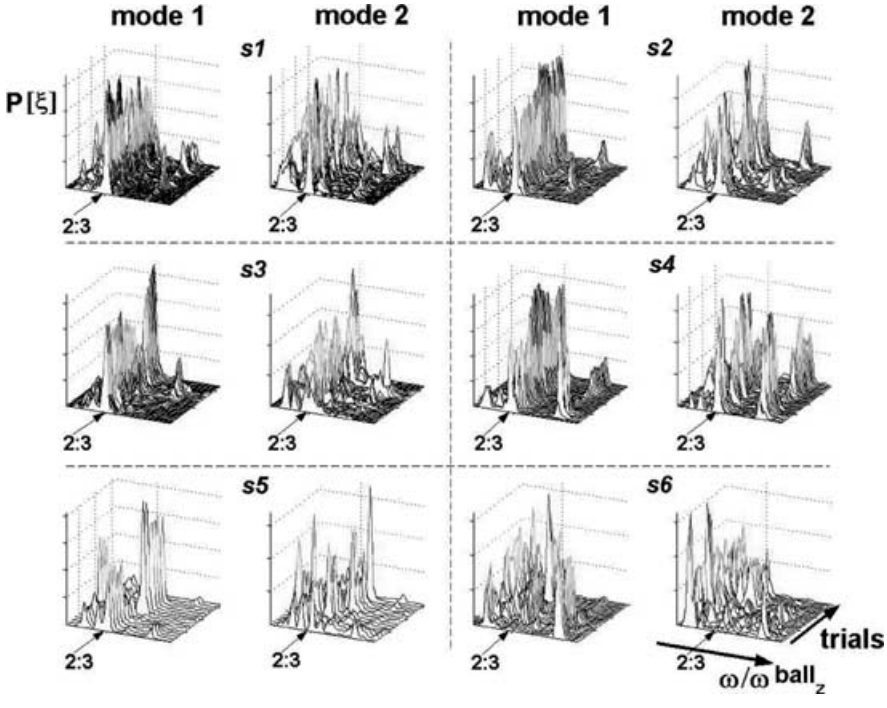

Fig. 7. Power spectral densities ($P[\xi]$) of the projections onto the first two modes of AP-sway for the windowed PCA as a function of practice for each subject (Fig. 6). In contrast to Fig. 6 a 2:3 locking ratio between the ball movements in the vertical direction and AP-sway is considered as indicated by the *arrows*

this mode disappeared and was re-established later in learning. Initially, for two of these three subjects (s4, s6), the 1:3 frequency locking had been the most dominant. For three other subjects (s1, s2, s3), the 2:3 mode had been dominant throughout the entire experiment; for two of them (s2, s3), this dominancy increased in that the spectral peak corresponding to the 2:3 mode gradually increased.

In sum, the windowed PCA revealed that both AP- and ML-sway usually contained a number of modes that were frequency locked to the ball movements. Interestingly, abrupt changes in these correlations or modes were found that would have remained hidden when only the 'overt' temporal evolution of these processes would have been studied.

3.3 Correlation between ball movements and respiration

Even though certain frequency locking ratios between the ball movements and respiration were observed, they could not be attributed unambiguously to entrainment,

as the observed evolution of locking ratios simply might have been due to changes in juggling speed in the face of a fairly constant frequency of respiration.[7]

4 Discussion

The present experiment was conducted to examine the development of task-specific couplings among functional subsystems during the acquisition of a complex perceptual-motor task. Specifically, six subjects practiced juggling three balls in a cascade pattern while video, force platform, and respiration recordings were taken simultaneously on specific days during a twenty-day training period. In this section, we will discuss the implications of the present results for the expectations that we formulated in the *Introduction*. Subsequently, we will discuss the implications of these results for the development of a dynamical theory of perceptual-motor learning in the general discussion.

4.1 Task performance and realization

We expected juggling performance, operationalized in terms of the degree of fulfillment of the prevailing task constraints, to increase asymptotically as a function of practice. This expectation was largely confirmed. In the course of learning, the degree of frequency locking between the ball trajectories increased monotonically, while the variance of the $2\pi/3$ rad phase difference between the ball trajectories decreased monotonically. In general, performance improved asymptotically, implying that the rate of improvement decreased with practice. Thus, as was expected, learning to juggle may be described as a gradual convergence of performance onto the prevailing task constraints. Alternatively, in terms of principal component analysis, it may be described as a decrease of dimensionality of the originally 6D (planar) juggling pattern, due to increasing symmetry (phase locking) and smoothness (see Post et al. 2000 for the corresponding analytical and empirical arguments and Fig. 3).

Besides a reduction of the number of relevant variables due to learning, clear indications were found for a gradual convergence of performance onto 'essential' variables. For instance, the pronounced differences in the (lag-two) correlation structure between 'temporal' and 'spatial' components suggest that the latter are less important for error correction, and that, hence, timing might be more essential in juggling than the control of spatial features (see also Post et al., 2000). Nevertheless, the CV of discrete spatial variables pertaining foremost to the ball movements also decreased significantly in the course of learning, whereas such an effect was absent in the CV of the spatial variables pertaining foremost to the hand movements (Van Santvoord 1995). Since the goal of juggling performance is defined primarily in terms of ball trajectories (i.e., keep a given number of objects aloft), rather than the movements of the end-effectors sustaining those ball trajectories, these results are consistent with the theoretical concepts of Scholz et al. (2000), who suggested that control converges onto those variables that are (most) essential for the task at hand. Or, to put it differently, the control of the individual hand movements in juggling is subordinate to the overarching task goal of circulating a number of objects as fluently as possible. In this light, we also interpret the negative lag-one auto-correlations that we found for the temporal and spatial properties of successive catches: by continuously adjusting the 'when' and 'where' of the catches (as well as the 'where' of the throws) small imperfections in the juggling pattern are quickly smoothed out. Although no evidence was found that these (discrete) error correction mechanisms improved in the course of learning, the ball trajectories clearly became 'smoother' as learning progressed; this was evidenced, for instance, by the diminishing relative contribution of the sub- and super-harmonics.

4.2 Task performance and postural sway

We expected the arm movements to become functionally embedded in the CoP-components, leading to the emergence of task-specific patterns of frequency locking with the ball movements. This expectation was confirmed, at least to some extent: using the windowed PCA technique it was shown that specific patterns of frequency locking (i.e., 2:3 and 1:3) were present between the ball movements and the CoP-trajectories, whereas the spectral analyses revealed unequivocally that the expression of these dynamics were often not dominant. To account for the frequency locking observed in the present study, we analyzed, in retrospect, a 3D mechanical model for the reflection of the arm movements in the sway components.

An important feature of the model is that the coupling between the arm movements and body sway is

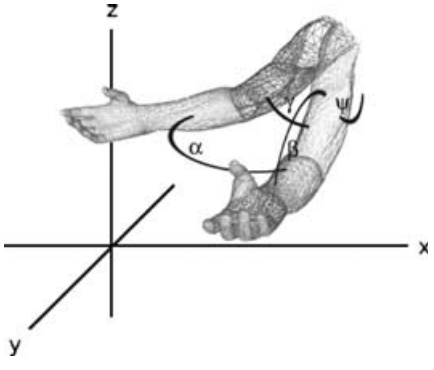

Fig. 8. 3D representation of 2-segment arm model (see text and Appendix)

[7] In the present study, frequency locking between the sway components and respiration could have been addressed. Any such analysis, however, would have suffered from a similar ambiguity as the analysis of the coordination between the ball movements and respiration because ball movements and body sway are frequency locked.

assumed to be unidirectional. This seems to be supported by the present data because the arm movements are clearly traceable in the sway trajectories, whereas the converse is not the case. Hence, when focusing exclusively on the arm movements one has to include at least four periodically changing angles (α, β, γ, and ψ), which, due to the task constraints, are interdependent (see Fig. 8 and Appendix for more mathematical details). As shown in the Appendix, when both arms oscillate perfectly in-phase in terms of α and γ and in anti-phase in terms of β and ψ, as in a well performed juggle, the resulting force projections on the AP-sway are frequency locked by a ratio of 2:3, whereas for ML-sway the locking ratio can be 1:3 or 2:3, depending on the amplitude of the arm movements. Hence, in line with the variability observed in the sway data, the model can illustrate how relatively small changes in the realization of juggling (e.g., arm amplitude) may have a considerable effect on the CoP-dynamics in that they may induce a switch in the dominance of the first and second harmonic. Notice, that changes in the magnitudes of the angles involved do not affect the ratio at which the AP-sway is frequency locked assuming an ideal left/right symmetry. Once such symmetry assumptions are dismissed, however, one can, for instance, observe switches from 2:3 to 1:3 (as provided by a change of the phase relation or offset; see Appendix for further details).

It is important to note, that although the magnitudes of the elbow angles and their spatial symmetry may induce a shift in the frequency locking, they do not necessarily affect the degree to which the prevailing task constraints are satisfied. Put differently, postural sway may be organized differently (both between and within individuals) in juggling performances of similar quality. The capacity to satisfy similar goals by different means (i.e., motor equivalence) thus not only pertains to the realization of a task involving different end-effectors, but extends to distinct coordination modes among end-effectors and the subsystems supporting the operation of those end-effectors.

Irrespective of the substantial trial-to-trial variability of postural sway, its dynamics underwent a structured, albeit hidden, evolution in the course of learning. In two subjects this evolution consisted of a rather abrupt switch from 1:3 frequency locking between the ball movements and AP-sway to 2:3 frequency locking, which was the only mode present during the final stage of the experiment. Whereas this may be viewed as evidence for a convergence of the sway dynamics to a common pattern in the course of learning (at least for the small number of subjects participating in the present study), the observation of abrupt mode transitions in two of the subjects suggests the presence of differential, individual-specific learning dynamics. Similar learning-induced mode transitions were observed in the context of both bimanual (Zanone and Kelso 1992, see *Introduction*) and postural coordination (Marin et al. 1999). In the latter study, the mode transition from in-phase ankle and hip rotation to anti-phase occurred at a higher frequency for the elite gymnasts than for the non-gymnasts – an effect that was ascribed to training (anti-phase coordination allows for larger hip movement amplitudes, which is penalized by gymnast judges). Clearly, in the Zanone and Kelso study the coordination mode adopted after the 'phase' transition was prescribed by the task, whereas in the study of Marin et al. the increased stability of in-phase coordination was the result of years of dedicated training in the absence of explicit instructions regarding the required hip-ankle coordination. The abrupt shifts in frequency locking observed in the present experiment seem more akin to the latter (largely implicit) than to the former (explicitly prescribed) phase transitions. It remains to be decided, however, whether these shifts are phase transitions in the sense of theories of self-organization or, alternatively, just a mechanical consequence of the molding of the sway dynamics through the performance of the supra-postural juggling task.

The evolutions of juggling performance and the sway dynamics were clearly different: whereas juggling performance increased gradually, the sway dynamics of a given individual either changed gradually or abruptly in the course of learning. Theoretical arguments for the occurrence of such a mixture of gradual and abrupt changes in learning were recently advanced by Newell, Liu and Mayer-Kress (2001), who proposed a framework for studying motor learning which is entirely consistent with the results of the present study. In addition to the existence of multiple coordination modes between ball movements and body sway, these non-parallel learning effects suggest that the postural control system remains relatively autonomous as it becomes embedded in a task-specific functional organization. In sum, forces and moments introduced by the juggling motions may, to a certain degree, shape the sway dynamics that may be differentially organized while subserving qualitatively similar performances.

4.3 Juggling and respiration

Our motivation for investigating the coordination between ball movements and respiration in juggling was that this activity is well suited to examine whether motor-respiratory couplings may be due to coordinative rather than biomechanical or energetic principles, as is more commonly assumed. After all, in juggling the mechanical forces impinging on the thorax and diaphragm as well as the corresponding aerobic demands are much smaller than in locomotion. Although we observed instances of frequency locking between the ball movements and respiration, these could not be ascribed unambiguously to entrainment. In this sense, the present results may be viewed as support for biomechanical or energetic explanations of LRC, although it cannot be ruled out that the present experiment was simply too short for such couplings to develop. It is well known that phylogenetically older systems, such as the respiratory system, are less adaptive than the younger structures, which is consistent with the observation that in general, LRC is observed in highly-trained runners (Bramble and Car-

rier 1982) and rowers (Mahler et al. 1991), but not in untrained athletes. Against this background, it might be useful to examine this issue further in a much longer longitudinal study of learning to juggle

5 General discussion

Various functional subsystems are implicated in the performance of complex perceptual-motor actions. In line with the theoretical intuitions of Bernstein (1996) and others, we assumed that, in the course of learning a particular perceptual-motor action, such subsystems become embedded to form a task-specific dynamical organization. We examined this theoretical assumption in the context of three-ball cascade juggling by examining the relation between the manipulations of the balls on the one hand and posture and respiration on the other. Whereas postural sway became embedded in clearly distinct dynamical modes, subserving performances of similar quality, respiration was not, or at best weakly coupled to the ball movements. The present findings regarding the coupling between ball movements and body sway are similar in spirit as our findings with regard to the coupling between ball movements and point of gaze in juggling (Huys and Beek 2002). In this particular study, it was found that differentially skilled jugglers' looking behaviors were either directly coupled to the ball movements (in one of two distinct ways) or largely uncorrelated with the ball movements. The more proficient jugglers adopted the direct coupling mode less often than the less proficient jugglers, while increases in juggling tempo resulted in weaker mode locking between point of gaze and the ball movements, as did simplifying the juggling pattern. Combining these observations with the present results suggests that, as functional subsystems become embedded in a task-specific organization, they maintain a certain degree of autonomy relative to this organization. This allows for the manifestation of a variety of dynamical signatures within the realization of the same task goal (motor equivalence). Besides skill level and 'inherent dynamics' of the systems under scrutiny, the actual manifestation of a particular coordination pattern probably also depends on the functional bearing of the subsystems on the realization of the task goal. That is, if the subsystems are directly 'responsible' for performance, such as the hands in juggling, only a highly specific and tightly coupled coordination will lead to (a high degree of) satisfaction of the task constraints. In contrast, for subsystems having only an indirect bearing on performance, such as posture or the visual tracking system, looser couplings, compatible with a diversity of dynamical modes, may be more beneficial as they may more readily allow for adaptation to changing circumstances. For example, when cycling, both hands have to be coordinated in a highly specific and coherent manner in order to by-pass cars, pedestrians and so forth, let alone to prevent falling. To be able to pickup ambient information about the traffic, however, it is to be preferred that the eyes are only loosely coupled to the hands.

The learning dynamics of postural sway and juggling performance differed qualitatively. This observation not only underscores the relative independence of the subsystems, but also suggests that, in the development of task-specific organizations, distinct, relatively autonomous processes may be operative, possibly at different, characteristic time scales. Indeed, studying such characteristic times in more detail can be quite challenging as it might allow for the detection of (distinct) processes as functional organization develops. Paraphrasing Bernstein's (1996) insights regarding the development of dexterity, practice results in a re-organization in that specific subtasks are assigned ('delegated') to those subsystems that are best suited to carry out those subtasks. One may suggest that behavioral convergence onto the more 'functional' variables, as observed in the present study, may go hand in hand with such biological re-organization. Furthermore, since different subsystems serve different subtasks, convergence onto the more useful variables may be a process that plays a role both within and among the subsystems. In this spirit, Huys and Beek (2002) suggested the increasing independence of expert jugglers to visually track the ball motions to be a result of confining the control space of juggling to variables associated with the hand movements. At first blush, the proposed convergence appears to be in line with claims that 'expertise reduces the number of solutions available in the perceptual-motor works-space' (Marin et al. 1999). As a counterpoint to this of view, however, our results may be interpreted to imply that with the utilization of more 'essential' variables the number of available (stable) solutions increases, rendering performance more flexible (see also Scholz and Schöner 1999). After all, besides stability and reproducibility, flexibility is a hallmark property of dexterity.

Appendix

We consider changes in the (force) projections onto the horizontal support plane due to rotations of the arms, represented as a 2-link segment (see Fig. 8). Furthermore, we assume these changes to be proportional to the evolution of the CoP-trajectories. α and β represent the angles of forearm rotation in the xy-plane and in the yz-plane, respectively, while γ and ψ are the angles of upper arm rotation in the xz-plane and in the zy-plane, respectively. All the angles, say φ, are assumed to evolve like $C \cdot \sin(\omega t) + \varphi_{\text{offset}}$, where the constant C is the magnitude (or amplitude) of rotation and the offset φ_{offset} allows for eventual asymmetries. Relative phasing between the left and right segment is denoted by $\Delta\varphi$ and L_{ua} and L_{fa} refer to the length of the upper arm and forearm, respectively.

The first component affecting ML-sway is due to a rotation of the forearm around α. The corresponding momentum depends on the 'effective' length of the forearm and is, hence, a function of the forearm rotation around β. In detail, we find

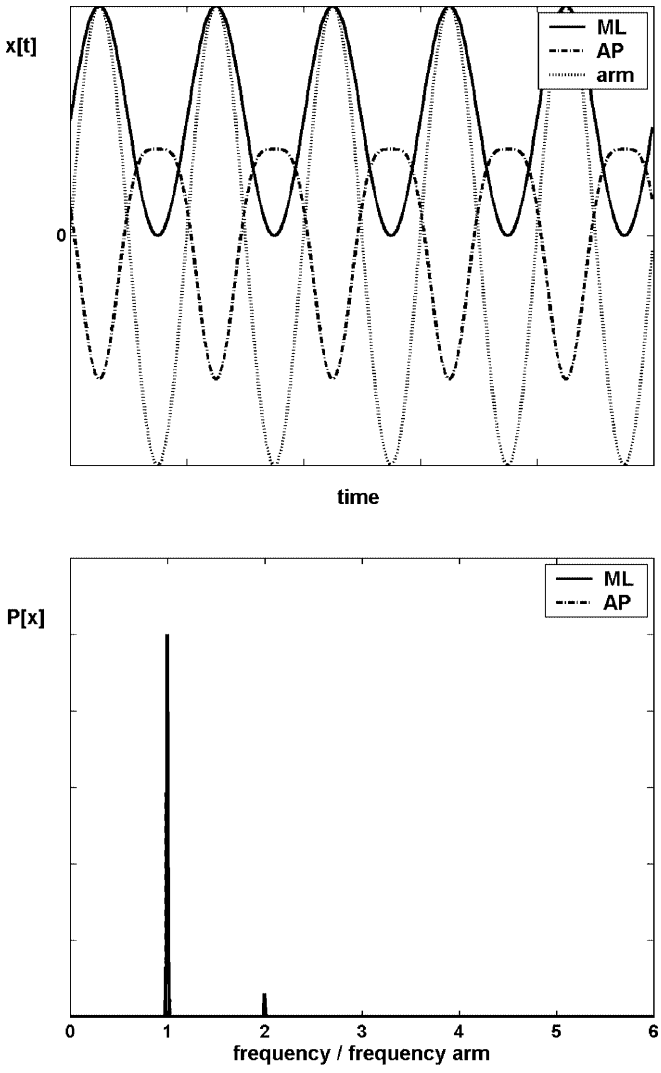

Fig. A1. Simulated time series of arm movements and ML- and AP-sway (*upper panel*) and their corresponding spectral densities (*lower panel*; sway components only). The arm movements are 1:1 frequency locked with both sway components; recall that for juggling performance this implies a 2:3 locking with the vertical ball trajectories (see text)

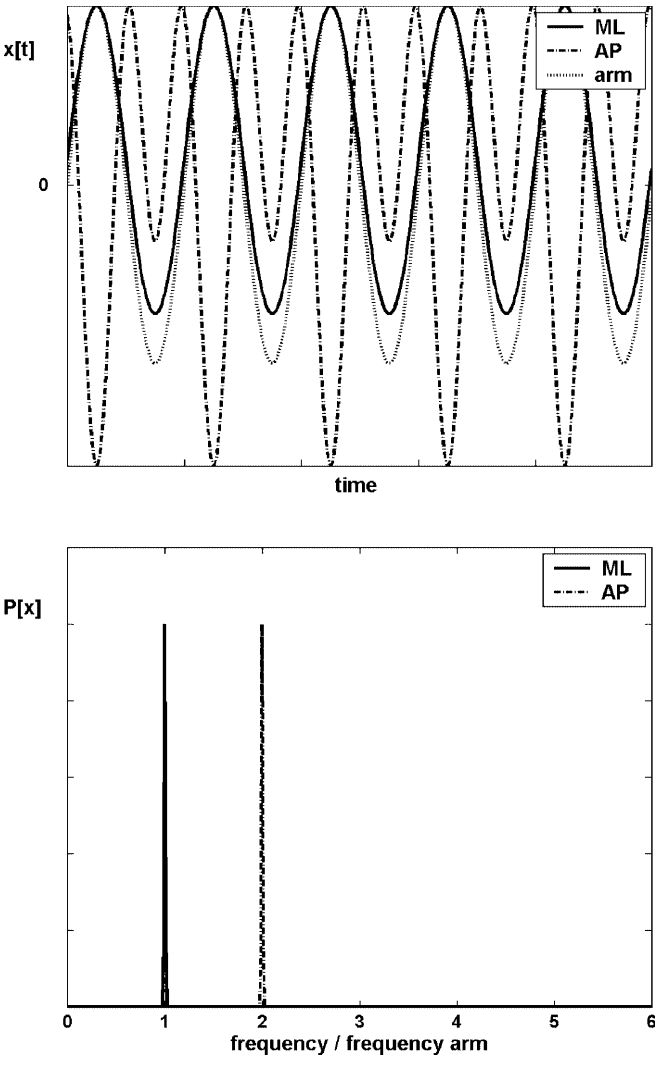

Fig. A2. Simulated time series of arm movements and ML-and AP-sway (*upper panel*) and corresponding spectral densities (*lower panel*; sway components only). The arm movements are 1:1 frequency locked with ML-sway and 1:2 with AP-sway; implying, for juggling, a 2:3 locking and a 1:3 locking with the vertical ball trajectories, respectively (see text)

$$ML_1(t) = L_{\mathrm{fa}} \sin(a \sin(\omega t) + \alpha_{\mathrm{offset}}) \cos(b \sin(\omega t) + \beta_{\mathrm{offset}}) + L_{\mathrm{fa}} \sin(a \sin(\omega t + \Delta\alpha) + \alpha_{\mathrm{offset}}) \cos(b \sin(\omega t + \Delta\beta) + \beta_{\mathrm{offset}}) \quad \text{(A1a)}$$

Second, the ML-sway is affected by the rotation of the upper arm around γ

$$ML_2(t) = L_{\mathrm{ua}} \sin(c \sin(\omega t) + \gamma_{\mathrm{offset}}) + L_{\mathrm{ua}} \sin(c \sin(\omega t + \Delta\gamma) + \gamma_{\mathrm{offset}}) \quad \text{(A1b)}$$

Note that γ is always positive because of the rheonomic constraint due to the torso; thus we have $c \geq \gamma_{\mathrm{offset}}$. In sum, the ML-sway is given by

$$ML(t) = ML_1(t) + ML_2(t) \quad \text{(A2)}$$

Similarly, in the AP-direction, rotation of the forearm around β will generate a sway inducing momentum as a function of the 'effective' length of the forearm:

$$AP_1(t) = L_{\mathrm{fa}} \cos(a \sin(\omega t) + \alpha_{\mathrm{offset}}) \cos(b \sin(\omega t) + \beta_{\mathrm{offset}}) + L_{\mathrm{fa}} \cos(a \sin(\omega t + \Delta\alpha) + \alpha_{\mathrm{offset}}) \cos(b \sin(\omega t + \Delta\beta) + \beta_{\mathrm{offset}}) \quad \text{(A3a)}$$

The second component is due to upper arm rotation around ψ yielding

$$AP_2(t) = L_{\mathrm{ua}} \sin(d \sin(\omega t) + \psi_{\mathrm{offset}}) + L_{\mathrm{ua}} \sin(d \sin(\omega t + \Delta\psi) + \psi_{\mathrm{offset}}) \quad \text{(A3b)}$$

and we find the total AP-sway as

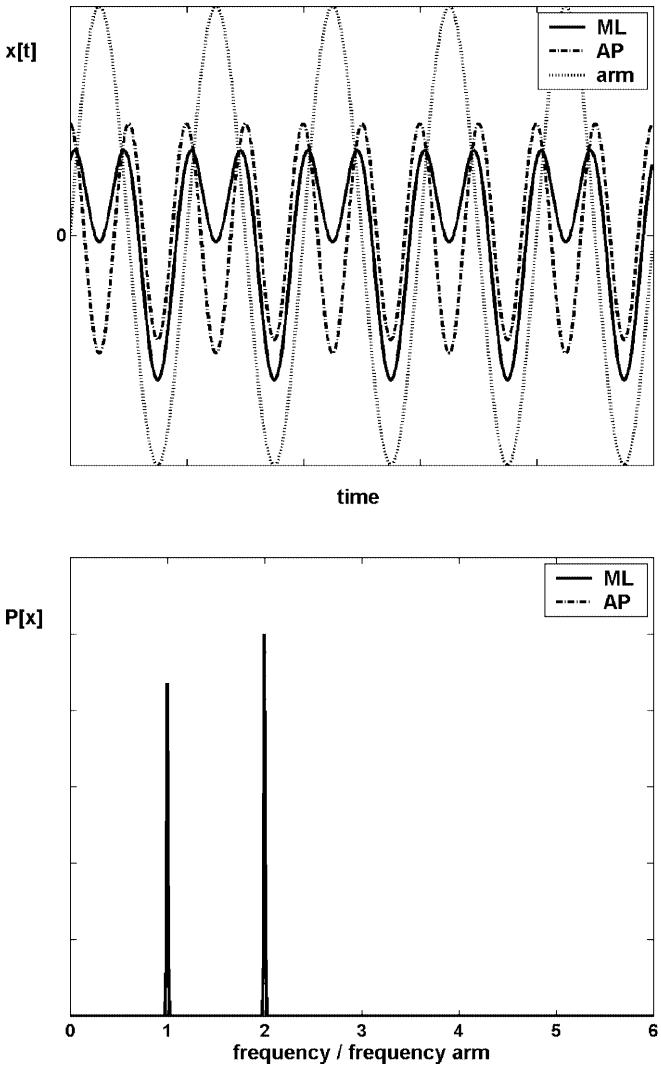

Fig. A3. Simulated time series of arm movements and ML-and AP-sway (*upper panel*) and corresponding spectral densities (*lower panel*; sway components only). The arm movements are 1:2 frequency locked with both sway components, implying, for juggling, a 1:3 frequency locking with the vertical ball trajectories – note that in all simulations (Figs. A2–A4) we used the same frequency of the arm movements

$$AP(t) = AP_1(t) + AP_2(t) \tag{A4}$$

When considering our empirical findings we need to estimate parameter ranges in which one may observe ML- and AP-oscillations with a frequency of either ω or 2ω. In fact, we can assume that all angle oscillations are reasonably small so that it becomes possible to concentrate on the Taylor expansions of (A2) and (A4). Expanding up to the third order around $\{a, b, c\} = \{0, 0, 0\}$ we get

$$\begin{aligned} ML(t) \approx\ & ML_0 + ML_1^{(1)} \cos(\omega t) + ML_1^{(2)} \sin(\omega t) \\ & + ML_2^{(1)} \cos(2\omega t) + ML_2^{(2)} \sin(2\omega t) \end{aligned} \tag{A5}$$

and for the expansion around $\{a, b, d\} = \{0, 0, 0\}$ it follows that

$$\begin{aligned} AP(t) \approx\ & AP_0 + AP_1^{(1)} \cos(\omega t) + AP_1^{(2)} \sin(\omega t) \\ & + AP_2^{(1)} \cos(2\omega t) + AP_2^{(2)} \sin(2\omega t) \end{aligned} \tag{A6}$$

Obviously, the constants $ML_1^{(1,2)}$ and $ML_2^{(1,2)}$ ($AP_1^{(1,2)}$ and $AP_2^{(1,2)}$) determine the relation between first and second harmonics and, thus, the relative strength of sway oscillations at 2ω. For the sake of legibility let us consider the special case in which we fix the relative phasing to $\Delta\alpha = \Delta\gamma = 0$ and $\Delta\beta = \pi$ (left and right symmetry). Then, for the harmonics of the ML-sway we obtain the constants

$$\begin{aligned} & \frac{1}{2}\sqrt{\left[ML_1^{(1)}\right]^2 + \left[ML_1^{(2)}\right]^2} \\ & \quad = \left| L_{\mathrm{fa}} a \cos\alpha_{\mathrm{offset}} \cos\beta_{\mathrm{offset}} + L_{ua} c \cos\gamma_{\mathrm{offset}} \right| \\ & 2\sqrt{\left[ML_2^{(1)}\right]^2 + \left[ML_2^{(2)}\right]^2} \\ & \quad = \left| L_{\mathrm{fa}} \left(a^2 + b^2\right) \sin\alpha_{\mathrm{offset}} \cos\beta_{\mathrm{offset}} \right| \end{aligned} \tag{A7}$$

and similarly for the AP-sway coefficients with $\Delta\alpha = 0$ and $\Delta\beta = \Delta\psi = \pi$

$$\begin{aligned} & \frac{1}{2}\sqrt{\left[AP_1^{(1)}\right]^2 + \left[AP_1^{(2)}\right]^2} = \left| L_{\mathrm{fa}} a \sin\alpha_{\mathrm{offset}} \cos\beta_{\mathrm{offset}} \right| \\ & 2\sqrt{\left[AP_2^{(1)}\right]^2 + \left[AP_2^{(2)}\right]^2} = 0 \end{aligned} \tag{A8}$$

Hence, in the fully symmetric case the AP-component will always oscillate with the basic harmonics, i.e., $\propto \sin(\omega t)$ or $\propto \cos(\omega t)$, whereas dependent on the lengths of the two body segments and the rotation amplitudes a, b, and c, the ML-components can optionally show a frequency doubling (in particular if $a = c = 0$ and $b \neq 0$). Note that one loop of a single ball in the vertical direction corresponds to three arm rotations. Thus, a CoP-oscillation at the basic harmonics of the arm constitutes a 2:3 frequency locking between the ball trajectory in the vertical direction and the CoP-trajectory.

To verify these analytical results we further studied the original model equations (A2) and (A4) numerically. As shown in Fig. A1 the case of full symmetry may indeed result in oscillations of both CoP-components with just the basic harmonics (we used $a = \alpha_{\mathrm{offset}} = 0.1$; all other parameters vanish). As soon as we leave the domain of very small amplitudes, however, we can easily obtain a frequency doubling as shown in Fig. A2 (there we used $a = 0.3$ and all remaining parameters are identical to Fig A1.) and Fig. A3 (using $a = 0.1$, $b = 0.4$, $\alpha_{\mathrm{offset}} = 0.25$, $\beta_{\mathrm{offset}} = 0.02$ and the other parameters identical to Fig. A1). These results highlight that a rather simplistic mechanical model of the arm movements may explain the various frequency locking ratios observed in the experiment.

Since the ball movements were only recorded in 2D future empirical work is needed to test the model in more detail.

Acknowledgements. The authors would like to thank an anonymous reviewer for helpful comments on earlier versions of this manuscript and Ivo Theunissen for graphical assistance. This research was supported by the Netherlands Organization for Scientific Research (NWO), Grant 425-202-01.

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